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Influence of Landscape Pattern on Habitat Use by American Marten in an Industrial Forest

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Abstract: Few studies have examined the potential for clearcutting to fragment habitat of area-sensitive, forest-dependent mammals such as American marten (*Martes americana*). We examined relationships among measures of landscape pattern and spatial use of habitat by 33 resident and 32 nonresident, adult marten that were radio-monitored in an extensively logged landscape. Size and distribution of forest patches (trees over 6 m in height) were associated with patch use by marten. Patches of forest used by resident marten (median = 27 ha, $n = 12$) were larger ($p < 0.003$) than patches with no observed use (median = 1.5 ha, $n = 128$). Further, patches used by residents were closer to the nearest patch larger than 2.7 ha (38 m versus 55 m; $p = 0.057$) and to an adjacent forest preserve (2.5 km versus 3.5 km; $p = 0.075$) than patches with no observed use. At four spatial scales (10, 65, 125, and 250 ha), grid cells used by resident marten comprised a greater percentage of residual forest over 6 m in height ($p \leq 0.008$) and intersected forest patches of greater area ($p \leq 0.006$) than cells with no observed use. Edge indices were not different ($p \geq 0.490$) between used grid cells and cells with no observed use at any of the four spatial scales. Analyses of forest edge associations indicated that marten did not avoid residual-regenerating forest edge within home ranges or within the study area. Home ranges ($n = 27$) of all resident, adult marten were composed of more than 60% forest cover over 6 m in height; median values were 78–80% for both sexes. The median size of the largest forest patch in marten home ranges was 150 ha for females and 247 ha for males. Our results suggest that reducing fragmentation by consolidating clearcuts and retaining large residual patches would help to maintain resident marten in extensively logged landscapes.

Influencia del Patrón del Paisaje en el Uso del Hábitat por la Marta Americana en un Bosque Industrial

Resumen: Pocos estudios han examinado el efecto de la tala en hábitats fragmentados de mamíferos sensibles al área y dependientes del bosque como lo es la marta americana (*Martes americana*). Examinamos las relaciones entre mediciones de patrones del paisaje y uso espacial de hábitat por 33 martas adultas residentes y 32 no residentes monitoreadas por radiotelemetría en un paisaje extensivamente talado. El tamaño y la distribución de parches de bosque (árboles > 6 m de altura) fueron asociados con parches usados por las martas. Los parches de bosque usados por martas residentes (mediana = 27 ha, $n = 12$) fueron mayores ($p < 0.003$) que los parches en los que no se observó uso (mediana = 1.5 ha, $n = 128$). Asimismo, los parches usados por residentes estuvieron más cerca a parches mayores de 2.7 ha (38 vs. 55 m; $p = 0.057$) y a bosques adyacentes conservados (2.5 km vs. 3.5 km; $p = 0.075$) que los parches en los que no se observó uso. A cuatro escalas espaciales (10, 65, 125 y 250 ha) las celdas usadas por las martas residentes comprendieron un porcentaje mayor de bosque residual >6 m de altura ($p \leq 0.008$) y de parches que interceptaron bosque de área mayor ($p \leq 0.006$) que las celdas en las que no se observó. Los índices de borde no fueron significativamente diferentes ($p \geq 0.49$) entre celdas usadas y las celdas que no mostraron uso a ninguna de las cuatro escalas espaciales usadas. Los análisis de asociaciones en el borde del bosque indicaron que las martas no evitaron bordes de bosque residual en regeneración dentro de los rangos de hogar o dentro del área de estudio. Los rangos de hogar ($n = 27$) de todas las martas residentes estuvieron compuestos por un 60% de cobertura forestal >6 m de altura; los valores de la mediana para ambos sexos estuvieron entre 78 y 80%. El valor de la mediana para los parches de bosque mas grandes usados por las martas fue de 150 ha para hembras y 247

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ba para machos. Nuestros resultados sugieren que la reducción de la fragmentación al consolidar la tala intensiva y retener parches residuales grandes podría ayudar a mantener poblaciones de martas residentes en paisajes talados extensivamente.

Introduction

The American marten (*Martes americana*) generally is considered an associate of mature forest habitat (Buskirk & Powell 1994), and alteration of forests via clearcutting has been temporally linked to the extirpation or decline of some marten populations (Bergerud 1969; Dodds & Martell 1970; Davis 1983). In Maine 70% of the occupied range of marten is owned by the forest products industry, which traditionally has used clearcutting as a common management practice. Studies of the effects of clearcutting on marten have reported selection against regenerating forest types (Steventon & Major 1982; Snyder & Bissonette 1987; Frederickson 1990; Katnik 1992) or reduced density of marten in logged versus unlogged landscapes (Soutiere 1979; Bissonette et al. 1989; Phillips 1994; Thompson 1994). The association of marten with mature, closed-canopy forests has been postulated to result from decreased risk of predation (Hargis & McCullough 1984; Drew 1995), increased abundance of subnivean resting sites (Steventon & Major 1982; Wynne & Sherburne 1984; Buskirk et al. 1989; Corn & Raphael 1992), and increased availability of prey (Soutiere 1979; Bateman 1986; Sherburne & Bissonette 1994; Thompson & Colgan 1994) relative to early-successional forests.

Despite the potential for clearcutting to fragment habitat of area-sensitive, forest-dependent mammals such as marten (Bissonette et al. 1989; Brainerd 1990; Buskirk 1992; Buskirk & Powell 1994), few data exist to evaluate the influence of landscape pattern on use of timber-harvested landscapes by marten (Snyder & Bissonette 1987; Hargis 1996; Hargis & Bissonette 1997). Quantitative relationships between landscape pattern and spatial use of habitat are needed to evaluate whether forest carnivores perceive industrial forest landscapes as fragmented at scales such as the forest patch and the individual home range, and to improve landscape-scale management of forested habitats.

Characteristics of landscape pattern that might cause forest fragmentation include reduced patch area, increased isolation of patches, and increased amount of edge (Harris 1984; Forman & Godron 1986; Hunter 1990), yet few empirical data are available from forest landscapes managed for timber production (Hagan et al. 1996). As forest fragmentation increases in agricultural landscapes, the landscape matrix shifts from forest to open land (Forman & Godron 1986). In forests managed for timber production, clearcutting may result in a matrix of regenerating forests with remnant forest patches that vary in age, area, isolation, shape, and amount of

edge (Franklin & Forman 1987). At the scale of the metapopulation, patch area and population persistence are predicted to be positively related, with smaller patches having fewer individuals, higher extinction rates, and lower colonization rates (Fahrig & Merriam 1994). Within a local population, patches that are small relative to home range requirements may receive little or no use by individual animals (Wilcove et al. 1986).

The effects of patch isolation depend largely on dispersal distance, migratory tendency, and habitat specificity of the species in question (Harris 1984). Patches may provide dispersal routes and facilitate dispersal of individuals (Fahrig & Merriam 1994; Boone & Hunter 1996), or isolation of patches may hinder dispersal and colonization (Smith 1974). Several studies (e.g., Soutiere 1979; Hargis & McCullough 1984; Snyder & Bissonette 1987; Drew 1995) have reported that marten seldom venture far into forest openings and that when they do they travel in a direct manner. The effect of distance to other patches on marten use of residual forest patches has not been documented, however.

Powell (1994) hypothesized that the presence of a mustelid in a habitat patch may cause a behavioral response of prey that depresses their vulnerability. Thus, if forest fragmentation results in more concentrated use of small, residual forest patches, then the capture success of marten may decrease because of prey conditioning. Further, if suitable patches are small relative to area requirements, individual marten may be unable to meet energetic needs or may choose an alternate area to maximize fitness. Although marten cross clearcuts to forage in residual forest patches, isolated patches may not provide adequate resources to warrant the risks associated with accessing them (Buskirk & Powell 1994; Drew 1995). For example, risk of predation may increase when marten travel across regenerating clearcuts that lack sufficient canopy or ground structure (Soutiere 1979; Snyder & Bissonette 1987; Thompson 1994; Drew 1995; Hodgman et al. 1997).

The influence of forest-clearcut edges on habitat quality for marten is unknown. Although Spencer et al. (1983) reported that marten selected for transitional forest-meadow edges at the scale of the habitat patch, the influence of edges on use intensity of forest patches has not been reported for areas where abrupt edges have been created via clearcut logging. Further, the association between density of edges and the occurrence of resident marten has not been quantified at the landscape scale. In contrast to the lack of data for most mammals, the effects of forest edge have been determined for

many species of birds (Yahner 1988). As the linear distance of edge increases relative to patch size, the area of patch interior decreases (Forman & Godron 1986). Thus, if marten avoid forest-clearcut edges, then suitable habitat could decrease nonlinearly when residual forests are logged (Bissonette et al. 1997). Further, some populations of small mammals used as prey by marten may be more diverse and abundant near ecotones (Yahner 1988), but some preferred species avoid ecotones (Mills 1995). Last, marten may avoid edges to minimize risks to predation (Drew 1995); potential predators such as coyotes (*Canis latrans*; Hodgman et al. 1997) concentrate foraging on edges (Harrison & Famous 1991).

Sandell (1989) suggests that, among solitary carnivores such as marten, female range size should be limited by resource availability and male range size should be limited by mate access. Buskirk and McDonald (1989), however, reported significant variation in home range area from studies across the geographic range of marten for males but not for females. Marten maintain extremely large home-range areas relative to their body weight compared to other carnivores (Buskirk & Ruggiero 1994); thus the ability of females to respond to habitat fragmentation by increasing home-range area may be physiologically constrained. Because marten are area-sensitive, forest-dependent carnivores and because the amount and spatial pattern of suitable habitat may be important determinants of home-range occupancy, conservation efforts should consider the spatial requirements of marten.

We assessed relationships between spatial characteristics of residual forest patches and use of habitat by marten in an industrial forest landscape in northcentral Maine characterized by extensive timber harvesting and intensive trapping. Our specific objectives were to (1) compare the area and extent of isolation of residual forest patches that received use by resident and nonresident marten with patches with no observed use; (2) compare the percent forest, size of forest patches, density of forest patches, and amount of edge within grid cells used by resident and nonresident marten with those with no observed use at multiple spatial scales; (3) evaluate the effects of forest edge on resident marten use of habitat within home ranges and within the study area; and (4) quantify the amount of regenerating forest and size of residual forest patches within the home ranges of resident marten.

Study Area

The study site was located in Piscataquis County, Maine, and was adjacent to the western boundary of Baxter State Park. Baxter State Park is an 814-km² wilderness area, 637 km² of which is closed to trapping and timber harvesting. The 132-km² study area contained three large water bodies (>40 ha), numerous small streams

(<3 m across), and mild topography with elevations from 290 to 565 m. The land was owned and managed for timber production by Great Northern Paper Co. and was characterized by a mosaic of forest stands over 6 m in height, from 0.08 to 3400 ha, interspersed with recently clearcut (harvested from 1982 to 1989) and regenerating forest (harvested from 1975 to 1982 and over 6 m in height); 46.7% of the study area had been clearcut (>75% canopy trees removed) since 1975.

Mature deciduous forests included sugar maple (*Acer saccharum*), red maple (*A. rubrum*), yellow birch (*Betula allegheniensis*), paper birch (*B. papyrifera*), and American beech (*Fagus grandifolia*). Mature coniferous forests were dominated by red spruce (*Picea rubens*) and balsam fir (*Abies balsamea*), with scattered white pines (*Pinus strobus*) occurring on well-drained sites. Forested wetlands included black spruce (*Picea mariana*), northern white cedar (*Thuja occidentalis*), and larch (*Larix laricina*). Regenerating clearcuts that were subsequently treated with the herbicide glyphosate (McCormack 1994) generally were characterized by dense regrowth of balsam fir and red spruce. Clearcuts that were not treated with herbicide generally were characterized by regenerating red maple, paper birch, pin cherry (*Prunus pensylvanica*), balsam fir, and red spruce. Raspberries (*Rubus* spp.) were present in all regenerating clearcuts.

Timber harvesting resulted in an extensive network of gravel roads (1.09 km of road/km²) that provided trappers with access to marten (Hodgman et al. 1994). Ninety percent of documented mortalities of radio-collared marten were caused by trapping (Hodgman et al. 1994).

Methods

Capture, Telemetry, and Home Ranges

Using the protocol described by Katnik et al. (1994), we live-trapped, aged, and radio-collared marten during spring (May–June) and autumn (September–October) of 1989 and 1990, and we radio-tracked them from May 1989 to April 1991. Our capture and handling protocol was approved by the Institutional Animal Care and Use Committee at the University of Maine, Orono. Approximately 25% of all trap sites were located in regenerating or recently cut forest, and adjacent trap sites were spaced less than 650 m apart to include all areas large enough to contain a marten home range (Katnik et al. 1994). We aged marten using *cementum annuli* and tooth radiographs (Katnik et al. 1994). We defined adults as marten that we determined to be at least 1 year of age, and we excluded juveniles (<1 year) from all analyses.

We attempted to locate each marten once each day from May to October using triangulation of three bearings from known positions on the ground separated in time by less than 60 minutes. The program TRIANG

(White & Garrott 1984) was used to compute the coordinates and size of the error polygon for each location. Locations with error polygons larger than 10 ha were excluded. Telemetry was also conducted from a fixed-wing aircraft in which we used two side-facing H-antennas and the methods of Gilmer et al. (1981). Observers recorded locations in flight on 1:16,000-scale aerial photographs.

Consecutive locations of individual marten were separated by at least 12 hours to maximize spatial independence of observations (Katnik et al. 1994; Phillips 1994). Of the 30 marten radio-collared during 1989, 21 were killed by trappers, 1 was killed by gunshot, and 2 died of natural causes prior to 1 January 1990. Only 138 telemetry relocations were obtained between November and April (Katnik 1992); therefore, we restricted our analyses to locations obtained from 1 May to 31 October (leaf-on season) of 1989 and 1990.

Based on area-observation curves, at least 30 locations per individual were needed to compute home-range areas that were independent of sampling intensity (Odum & Kuenzler 1955) for marten on our study site (Katnik et al. 1994). Thus, for marten with at least 30 locations, we calculated 95% minimum convex polygon (MCP) home ranges (Mohr 1947) using a program developed by Chapin (1995) that computed the smallest possible convex polygon surrounding 95% of all locations (White & Garrott 1990).

Study Site, Residency, and Habitat Database

We defined the study site as a concave polygon around all captures and relocations of resident adult marten that occurred within the area that was trapped in both 1989 and 1990, including areas that were trapped unsuccessfully (Fig. 1). We defined residents as marten with at least 30 locations that defended a territory for at least 3 months that overlapped with a resident of the opposite sex, or marten with 10–29 locations with an MCP that was smaller than the mean 95% MCP (4.70 km² for males, $n = 13$; 2.62 km² for females, $n = 14$) of marten with at least 30 locations obtained during at least 3 months, and that overlapped with at least 1 resident of the opposite sex. Thus, we included all potential residents with reproductive opportunities, including those with too few locations (<30 , Katnik et al. 1994), to compute home ranges. Marten with less than 10 locations, marten with 10–29 locations and exceptionally large MCPs, or marten that did not overlap the locations or home range of a resident of the opposite sex were classified as nonresidents. We hypothesized that transient individuals may have occupied lower-quality habitats than successfully breeding residents (Van Horne 1983); therefore, we analyzed residents and nonresidents separately.

Forest types were delineated from 1:15,840-scale color infrared aerial photographs taken in 1982. Areas harvested after typing were delineated from 1:80,000-

scale, black-and-white photographs taken in 1988 and were classified as recently cut forest. Areas harvested between 1974 and 1982 were classified as regenerating clearcuts. The habitat coverage was provided in digital format by the landowner and was incorporated into a vector-based geographic information system (ARC/INFO 3.4.1, Environmental Systems Research Institute, Redlands, California).

Patch Definition

We defined residual forest patches as contiguous areas composing adjacent stands of mid- to late-successional forest (>6 m in height and $>50\%$ canopy closure, or >12 m and $<50\%$ canopy closure). We defined regenerating forest as stands harvested since 1975. This categorization was based on Katnik's (1992) findings that home ranges of marten on our study site contained disproportionately more ($p < 0.05$) mid- to late-successional forest types (i.e., mature well-stocked, mature poorly stocked, and immature well-stocked) and disproportionately less recently cut, regenerating forest (<6 m) than occurred in the available landscape (i.e., landscape-scale habitat selection).

Patch Use

Using locations pooled across individuals, we categorized a forest patch as used if it contained at least 1 marten location. We analyzed data separately for resident and nonresident marten. Marten on our site were territorial (Katnik et al. 1994); therefore, we hypothesized that nonresident adults might exhibit different patterns of habitat selection and lower fitness than established residents.

Because of telemetry error, marten use of residual patches near the forest edge could result in telemetry locations occurring in regenerating forest, causing a disproportional underestimate of use in small patches. Based on the documented affinity of marten for mid- to late-successional forested habitat on our study site (Katnik 1992), we accounted for this potential bias by categorizing a residual forest patch as used if a location occurred within telemetry error of the edge of the residual forest patch.

We measured the size of each forest patch and the following measures of isolation: distance to the nearest residual forest patch, distance to the nearest patch larger than the minimum size of patches that contained at least one location (2.7 ha), and distance to an adjacent forest preserve. Distance to the nearest residual forest patch was measured using an edge-to-edge nearest neighbor distance. We used a Mann-Whitney test (Conover 1980) to compare measures of landscape pattern for used residual forest patches with those of patches that contained no locations; we analyzed data for marten that were classified as residents and nonresidents separately.

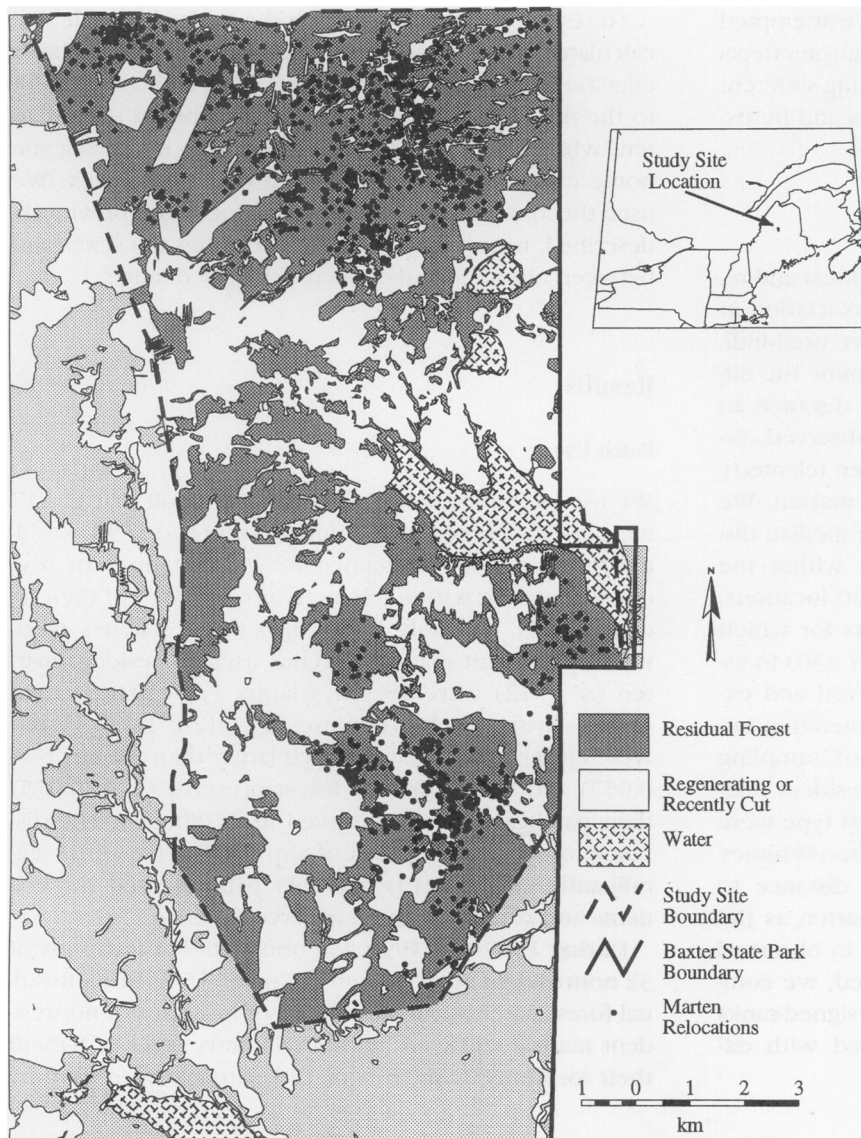


Figure 1. Residual forest patches, regenerating forest, and telemetry locations ($n = 1188$) of resident adult marten during the summers (1 May–31 October) of 1989 and 1990 in northcentral Maine.

Grid Cells

We overlaid four uniform grids on the study area with cell sizes equal to 10, 65, 125, and 250 ha. Using locations pooled for residents and nonresidents separately, we compared measures of landscape pattern between grid cells that were used (≥ 1 location) with those of cells that contained no locations at the four spatial scales. The rationale for establishing grid cell sizes was as follows: 10 ha was the largest error polygon for telemetry locations used in the analysis; 65 ha was approximately 25% of the average female home-range size ($\bar{x} = 2.6 \text{ km}^2$, $n = 14$); 125 ha was approximately 50% of the average female range size and 25% of the average male range size ($\bar{x} = 4.5 \text{ km}^2$, $n = 13$); and 250 ha was approximately equal to the average female range size and 50% of the average male range size. We excluded cells

that overlapped the study area boundary or a large water body.

For each grid cell we measured the percentage of the cell comprising residual forest, the size of the largest residual forest patch in the cell, the number of different residual forest patches in the cell, and an edge index. The edge index was calculated as one-fourth the sum of the perimeters of residual forest patches within the grid cell, including the cell perimeter, divided by the square root of the cell area (McGarigal & Marks 1995). For each spatial scale, we used a Mann-Whitney test to compare used grid cells with cells that contained no locations; resident and nonresident marten were compared separately.

Because of the exploratory nature of these analyses and despite the multiple, simultaneous comparisons being made, we used $\alpha = 0.10$ and pairwise p values to exam-

ine the strength of individual relationships. We attempted to account for spurious results by examining the effects of residual patch area, isolation, and edge using different measurements, techniques, and spatial scales and by examining the results for trends among analyses.

Edge Associations

We defined edge as boundaries between residual and regenerating forest types. To test for edge association at the stand scale (i.e., within home ranges), we used individual marten as the sampling unit to determine the difference between observed and expected distance to edge within home ranges. We computed observed distance to edge as the median distance between telemetry locations and forest edge for each resident marten. We computed expected distance to edge as the median distance to edge from 2000 random points within the home range of each resident with at least 30 locations; thus, the analysis was restricted to residents for which there were a sufficient number of locations (≥ 30) to estimate a home range. We measured observed and expected distance to edge in residual and regenerating forest separately. To reduce the influence of sampling variance on the median distance to edge, resident marten with less than 10 locations in either forest type were excluded from the analysis. We used Mann-Whitney tests to compare observed and expected distance to edge between sexes, treating individual marten as the sampling unit. If no sex-specific difference in observed or expected proximity to edge was detected, we combined data across sexes and used Wilcoxon signed-ranks tests (Conover 1980) to compare observed with expected distances for the pooled sample.

To test for edge association at the landscape scale, we calculated the density of residual-regenerating forest edge (km/km^2) within each home range and compared it to the density of edge in the area available to each marten, which we defined as the study site, excluding the home ranges of sympatric marten of the same sex. We used the Mann-Whitney/Wilcoxon procedure, previously described, to test for differences between the sexes and between observed and expected density of edge.

Results

Patch Use

We used 1188 locations of 33 resident adult marten (17 male, 16 female) collected during 1989 and 1990. Residual forest patches contained 82% of locations of residents and were within telemetry error of 96% of their locations (Fig. 1). Only 9% of 140 forest patches were used by resident marten. Patches used by resident marten ($n = 12$) were 18 times larger ($p = 0.003$) than patches with no observed use ($n = 128$; Table 1) and were closer to the nearest patch larger than 2.7 ha ($p = 0.057$) and to an adjacent forest preserve ($p = 0.075$) than patches with no observed use (Table 1). The distance to the nearest patch of any size did not differ significantly ($p = 0.219$) between patches used by residents and patches with no observed use.

During 1989 and 1990, we obtained 274 locations of 32 nonresident adult marten (17 male, 15 female). Residual forest patches contained 62% of locations of nonresident marten and were within telemetry error of 84% of their locations. Only 15% of 140 patches were used by

Table 1. Measures of landscape pattern for used versus unused residual forest patches for resident ($n = 33$) and nonresident ($n = 32$) adult marten during the summers (1 May–31 October) of 1989–1990 in northcentral Maine.

Landscape metric	Used ^a			Unused			p
	Median	25% quantile	75% quantile	Median	25% quantile	75% quantile	
Residents ^b							
n^c	12			128			
area (ha)	27.0	2.4	313.0	1.5	0.6	4.4	0.003
distance to nearest patch (m)	31	25	41	39	26	72	0.219
distance to patch >2.7 ha (m)	38	26	48	55	32	134	0.057
distance to preserve ^d (km)	2.5	0.2	3.4	3.5	1.6	5.1	0.075
Nonresidents ^e							
n^c	21			119			
area (ha)	7.9	1.9	140.0	1.5	0.5	3.0	<0.001
distance to nearest patch (m)	32	22	44	43	27	74	0.055
distance to patch >2.7 ha (m)	37	29	52	58	33	138	0.043
distance to preserve (km)	4.9	2.3	5.7	3.2	1.5	4.8	0.152

^aUsed patches contained at least one marten location or had a location within telemetry error of the patch edge.

^bMore than 10 locations and overlapping at least one resident of the opposite sex.

^cNumber of forest patches.

^dDistance to boundary of adjacent Baxter State Park, an untrapped forest preserve.

^eMore than 10 locations or not overlapping any resident of the opposite sex.

nonresidents. Patches used by non-resident marten ($n = 21$) were 5.3 times larger ($p < 0.001$) and were closer to the nearest residual forest patch ($p = 0.055$) and to the nearest patch larger than 2.7 ha ($p = 0.043$) than patches with no observed use ($n = 119$; Table 1). Distance to an adjacent forest preserve did not differ significantly ($p = 0.152$) between patches used by nonresidents and patches with no observed use.

Grid Cells

At all four spatial scales, grid cells used by resident adult marten contained a higher ($p \leq 0.004$) percentage of residual forest cover and had a larger ($p \leq 0.003$) maximum patch size than cells with no observed use (Table 2). At the 10-ha grid-cell size, used cells contained more ($p < 0.001$) patches than cells with no observed use; for the 125- and 250-ha grid cells, however, used cells contained fewer ($p \leq 0.085$) patches than cells that contained no locations (Table 2). At a 10-ha resolution, grid cells completely within regenerating forests contained no residual forest patches, reducing the median number of patches among unused cells. At an intermediate cell size (65 ha) there was no significant difference ($p = 0.134$) in number of residual forest patches between used cells and cells that contained no locations (Table 2).

For nonresident adult marten, used grid cells contained a higher proportion of residual forest cover ($p \leq 0.087$) than cells with no locations at the 10- and 65-ha cell sizes, but the difference was not significant ($p \geq 0.460$) at the 125- or 250-ha cell sizes (Table 2). Similarly, the

size of the largest residual patch in the cell was larger ($p \leq 0.049$) for used cells than for cells that contained no locations at the 10- and 65-ha cell sizes, but it did not differ ($p \geq 0.481$) at the 125- or 250-ha cell sizes (Table 2). The number of patches per cell did not differ ($p \geq 0.292$) between used cells and cells that contained no locations at any of the spatial scales examined (Table 2).

Edge Associations

We detected no difference in an edge index between used cells and cells that contained no locations at any spatial scale for either residents ($p \geq 0.587$) or nonresidents ($p \geq 0.271$, Table 2). Among locations occurring in residual forest, we detected no difference between resident adult males ($n = 13$) and females ($n = 14$) in observed ($p = 0.817$) or expected ($p = 0.628$) distance to residual-regenerating forest edge within their home range. Thus, we combined data on distance of marten to edges across sexes for subsequent analysis. For the subset of locations that occurred in residual forest, the observed distance to edge (median = 110 m) was less ($p = 0.049$, $n = 28$) than expected (median = 120 m), but the difference (10 m) was small relative to telemetry error. In regenerating forest, only seven males and three females had at least 10 locations, so we combined data for both sexes without testing for sex-specific differences. Among locations that occurred in regenerating forest, observed distance to edge (median = 25 m) did not differ ($p = 0.121$, $n = 10$) from expected (median = 45 m).

Table 2. Comparison of measures of landscape pattern (medians) between used and unused grid cells for resident ($n = 33$) and nonresident ($n = 32$) adult marten during the summers (1 May–31 October) of 1989–1990 in northcentral Maine.

Landscape metric	Grid cell size (ha) ^a											
	10			65			125			250		
	used	unused	p ^b	used	unused	p	used	unused	p	used	unused	p
Residents^c												
number of cells	354	835		83	78		49	30		24	12	
percent forest	85	33	<0.001	75	31	<0.001	66	30	<0.001	59	37	0.004
largest patch (ha) ^d	8.4	2.8	<0.001	42	15	<0.001	73	24	<0.001	137	50	0.003
number of patches/cell	1	1	<0.001	2	2	0.134	3	6	0.008	5	9	0.085
edge ^e	1.6	1.6	0.895	2.7	2.8	0.587	3.3	3.6	0.960	4.6	4.3	0.788
Nonresidents^f												
number of cells	129	1060		61	100		42	37		25	11	
percent forest	62	52	0.024	61	47	0.087	56	45	0.961	55	49	0.460
largest patch (ha) ^d	5.7	5.0	0.027	35	25	0.049	60	54	0.891	100	81	0.481
number of patches/cell	1	1	0.292	2	2	0.533	3	4	0.724	5	4	0.406
edge ^e	1.7	1.6	0.457	2.7	2.7	0.957	3.3	3.8	0.271	4.2	5.4	0.525

^aGrid-cell sizes were based on maximum telemetry error (10 ha) and 25%, 50%, and 100% of the mean resident adult female home-range size (2.6 km²).

^bMann-Whitney test.

^cMore than 10 locations and overlapping at least one resident of the opposite sex.

^dSize of the largest forest patch in the grid cell.

^eEdge index is 1 if no forest edge is in the grid cell and increases without limit as the amount of forest edge in the grid cell increases.

^fLess than 10 locations or not overlapping any resident of the opposite sex.

Observed density of edge in home ranges was not significantly different ($p = 0.846$) between males (median = 3.60, $n = 13$) and females (median = 3.71, $n = 14$), so we combined data across sexes. Density of edge within home ranges of resident adult marten (median = 3.6 km/km²) was not significantly different ($p = 0.269$, $n = 27$) from the density of edge in the available landscape (median = 4.4 km/km²).

Home-Range Characteristics

Regenerating forest composed a median of 22% (range 9–40%) of male home ranges ($n = 13$) and 20% (range 7–31%) of female ranges ($n = 14$). The largest residual forest patch in the home range composed a median of 75% (range 30–90%) of male ranges and 80% (range 51–93%) of female ranges; at least half of each female's range was composed of a single, contiguous residual patch. The median size of the largest residual patch in the range was 247 ha for males and 150 ha for females.

Discussion

Few of the available residual patches on our study site received use by resident marten, indicating that patch attributes may play an important role in determining habitat suitability. Home ranges of resident adult marten were associated with large, contiguous residual forest patches in the extensively clearcut landscape occurring on our study site. Across a range of spatial scales, the amount of residual forest and the size of patches were positively related to use of grid cells by resident marten. Both residents and nonresidents used residual patches much larger than those with no observed use. Thus, area was the most important characteristic of residual forest patches that influenced use by marten on our study site.

Area of residual patches also influenced marten use of forests in Newfoundland (Snyder & Bissonette 1987). Only 5 of 51 marten captures occurred in forest patches smaller than 15 ha; the authors concluded that larger (>15 ha) residual and undisturbed patches are important habitat components for marten in extensively clearcut areas. In earlier studies in Maine (Soutiere 1979), marten used residual forest patches within regenerating forests, but the relationship between patch use and patch area was not examined.

The central portion of our study area received no use by resident marten and little use by nonresidents and was generally characterized by numerous small patches that accounted for a low percentage of overall forest cover (Fig. 1). This suggests that isolation of residual patches interacts with patch size to influence the spatial distribution of marten in landscapes with extensive clearcutting. Some measures of patch isolation (i.e., distance to nearest patch larger than 2.7 ha and distance to

an adjacent forest preserve) suggested that unused patches were isolated from patches that were large enough to be used. Furthermore, although nonresidents exhibited greater variability in use of residual forest patches than did residents, patches used by nonresidents were significantly closer to the nearest patch of any size and the nearest patch over 2.7 ha. Thus, isolation from suitable residual patches may have contributed to the absence of locations of both residents and nonresidents in some portions of our study site.

Residual-regenerating forest edge did not seem to affect marten habitat use. The results of our grid-cell analysis suggest that the amount of edge did not influence marten distribution across a range of spatial scales. Although marten did not avoid edges while traveling in residual forest, our ability to detect differences between observed and expected distance to edge when marten were located in regenerating habitats was limited by the low use of those habitats, resulting in low statistical power ($n = 10$ animals with ≥ 10 locations in regenerating forest). Furthermore, the difference between observed and expected distance to edge was nearly significant ($p = 0.121$), suggesting that when marten use regenerating habitat they may tend to forage near the edge of residual forest patches. The density of edge did not seem to influence the distribution of marten on our study site; long, narrow strip cuts resulted in substantial amounts of edge in the home ranges of several marten that inhabited the northern portion of our study site (Fig. 1). The residual forest in this area remained contiguous and accounted for at least 60% of each resident home range.

Our conclusions that marten positioned their home ranges to minimize fragmentation from clearcut logging might be confounded if marten avoided placing home ranges near forest roads, which were constructed to facilitate logging. To the contrary, 27 of 28 resident marten with more than 30 locations each had forest roads accessible by two-wheel-drive vehicle within their home range. Furthermore, the median density of roads within home ranges of marten exceeded 0.8 km/km² (D.D.K., D.J.H., and T. Hodgman, unpublished data). Thus, we conclude that marten were responding more strongly to forest fragmentation associated with clearcut logging than to proximity to forest roads.

Our findings are consistent with Katnik's (1992) findings that habitat use by marten in our industrial forest site is influenced by the distribution of residual forest on the landscape. Katnik (1992) documented that resident adult marten exhibited landscape-scale selection against recently cut or regenerating clearcuts on our study site. Similarly, we documented that 96% of resident marten locations occurred within telemetry error of residual forest patches and that only 10 of 33 resident marten had more than 10 locations in regenerating forest. Katnik (1992), however, also concluded that, within home

ranges, marten used regenerating clearcuts in proportion to availability. Thus, marten used regenerating forest within their home ranges but established home ranges only in areas dominated by residual forest. For example, half of all resident marten home ranges comprised less than one-quarter regenerating forest, and no resident marten known to overlap with a resident of the opposite sex occupied a range with over 40% regenerating forest.

Population density of marten on our site was probably below carrying capacity, and marten may have occupied the best of the available habitats. Trapping on our study site reduced density annually by removing most resident adults and some dispersers, which may have established a territory the following year. None of the marten that Katnik et al. (1994) sampled in 1989 were recaptured in 1990, and trapping accounted for 90% of all documented mortalities (Hodgman et al. 1994). Phillips (1994), however, detected no difference in measures of population performance (i.e., percent lactating, home-range area, intrasexual overlap) among adult females on our study site compared with females in an adjacent, untrapped forest preserve, despite significantly lower densities. He concluded that females on our industrial forest site maintained productivity via landscape-scale habitat selection. Thus trapping, which is often associated with timber harvesting via trapper access on logging roads (Hodgman et al. 1994), may reduce marten population densities below the level at which habitat is limiting. At higher densities, marten may occupy a wider range of habitats, but measures of population performance should be considered before inferences are made about habitat quality (Van Horne 1983).

Conclusions and Management Implications

We defined residual forest patches as forest with height over 6 m and canopy closure over 50%, or height over 12 m and canopy closure less than 50%, based on results from a previous study on our site (Katnik 1992). This definition of residual forest may vary regionally because rates of succession, dominant tree species, and corresponding structural characteristics of forests vary across the geographic range of the marten. Therefore, an understanding of how marten relate to overstory species composition, canopy closure, forest age, and forest structure in a particular region is necessary to define forest patches before assessing the pattern of residual forest on the landscape. Further, the predominant silvicultural practice on our site was even-aged management via clearcutting. Alternative harvesting methods (e.g., selection cuts) may increase the use of harvested forests (Soutiere 1979; Steventon & Major 1982) and could reduce fragmentation of the landscape from the perspective of marten.

Populations of resident marten with reproductive potential can exist in extensively clearcut, intensively trapped landscapes if residual forest patches of sufficient size are maintained. Our data indicate that marten will use small residual patches but that much larger patches are required to support home ranges. Female home ranges (average size = 260 ha) contained mostly residual forest, of which a median of 150 ha composed a single contiguous patch. Males occupied home ranges (average size = 450 ha) dominated by a single contiguous patch with a median size of 247 ha. Despite different spatial requirements, both males and females tolerated a median of only 20% regenerating clearcuts in their home ranges, and maximum observed values were 40% and 31% for individual males and females, respectively. Similarly, Hargis and Bissonette (1997) reported that captures of individual marten in Utah declined to zero when openings occupied over 25% of the landscape. Social interactions among marten (e.g., intrasexual territoriality, polygyny) require that spatial requirements of the breeding unit (i.e., resident adult marten of the opposite sex with overlapping territories) be considered when recommendations for forest management are developed. Thus, habitat conservation that maintains viable breeding units would likely require larger forest patches than our data based on the spatial requirements of individual marten.

The minimum size of forest patches associated with home-range occupancy by resident marten may change in the absence of trapping or in areas where human access via forest roads is limited during the trapping season. But the threshold percentage of residual forest associated with home range occupancy by resident adult females that we observed (20–30%) may apply across the geographic range of marten and is consistent with thresholds documented for marten of both sexes in the intermountain west (Hargis & Bissonette 1997). No differences in female home-range size were observed between our study area and an untrapped forest preserve (Phillips 1994). Although home-range areas of male marten vary regionally, range areas of females are consistent throughout the species' geographic range (Buskirk & McDonald 1989), suggesting that, across a range of local habitat conditions, variability in female home-range area may be constrained by resource availability, morphology, and energetic demands. Further, our results reflect patterns of habitat occupancy by successful reproducers, which may further limit variability in percentage of residual forest among home-range areas; six of seven females at least 2 years of age on our study site were lactating when captured in spring (Phillips 1994). Given potential source-sink dynamics (Pulliam 1988) associated within a territorial species such as marten (Katnik et al. 1994), we recommend that spatial requirements of successfully reproducing adults should form the basis for landscape-scale conservation efforts.

We documented that forest fragmentation influenced the spatial use of habitat by resident adult marten in an industrial forest landscape with extensive clearcutting and intensive trapping. The most significant fragmentation effects were reduced patch area and increased patch isolation. Long-term planning to maximize residual patch area and minimize distance between large residual forest patches is recommended to maintain marten in forested landscapes with human disturbance.

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Literature Cited

- Bateman, M. C. 1986. Winter habitat use, food use, and home range size of the marten, *Marten americana*, in western Newfoundland. *Canadian Field-Naturalist* **100**:58–62.
- Bergerud, A. T. 1969. The status of pine marten in Newfoundland. *Canadian Field-Naturalist* **83**:128–131.
- Bissonette, J. A., R. J. Frederickson, and B. J. Tucker. 1989. American marten: a case for landscape-level management. *Transactions of the North American Wildlife and Natural Resources Conference* **54**:89–101.
- Bissonette, J. A., D. J. Harrison, C. D. Hargis, and T. G. Chapin. 1997. The influence of spatial scale and scale-sensitive properties on habitat selection by American marten. Pages 368–385 in J. A. Bissonette, editor. *Wildlife and landscape ecology: effects of pattern and scale*. Springer-Verlag, New York.
- Boone, R. B., and M. L. Hunter, Jr. 1996. Using diffusion models to simulate the effects of land use on grizzly bear dispersal in the Rocky Mountains. *Landscape Ecology* **11**:51–64.
- Brainerd, S. M. 1990. The pine marten and forest fragmentation: a review and general hypothesis. *Transactions of the Congress of the International Union of Game Biologists* **19**:421–434.
- Buskirk, S. W. 1992. Conserving circumboreal forests for martens and fishers. *Conservation Biology* **6**:318–320.
- Buskirk, S. W., and L. L. McDonald. 1989. Analysis of variability in home-range size of the American marten. *Journal of Wildlife Management* **53**:997–1004.
- Buskirk, S. W., and R. A. Powell. 1994. Habitat ecology of fishers and American martens. Pages 283–296 in S. W. Buskirk, A. S. Harestad, M. G. Raphael, and R. A. Powell, editors. *Martens, sables, and fishers: biology and conservation*. Cornell University Press, Ithaca, New York.
- Buskirk, S. W., and L. F. Ruggiero. 1994. American marten. Pages 7–37 in L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, L. J. Lyon, and W. J. Zielinski, editors. *The scientific basis for conserving forest carnivores: American marten, fisher, lynx, and wolverine in the western United States*. General technical report RM-254. U.S. Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado.
- Buskirk, S. W., S. C. Forrest, M. G. Raphael, and H. J. Harlow. 1989. Winter resting site ecology of marten in the central Rocky Mountains. *Journal of Wildlife Management* **53**:191–196.
- Chapin, T. G. 1995. Influence of landscape pattern and forest type on use of habitat by marten in Maine. M. S. thesis. University of Maine, Orono.
- Conover, W. J. 1980. *Practical nonparametric statistics*. 2nd edition. John Wiley & Sons, New York.
- Corn, J. G., and M. G. Raphael. 1992. Habitat characteristics at marten subnivean access sites. *Journal of Wildlife Management* **56**:442–448.
- Davis, M. H. 1983. Post-release movements of introduced marten. *Journal of Wildlife Management* **47**:59–66.
- Drew, G. 1995. Winter habitat selection by American marten (*Martes americana*) in Newfoundland: why old growth? Ph.D. dissertation. Utah State University, Logan.
- Dodds, D. G., and A. M. Martell. 1970. The recent status of the marten, *Martes americana americana* (Turton), in Nova Scotia. *Canadian Field-Naturalist* **85**:61–62.
- Fahrig, L., and G. Merriam. 1994. Conservation of fragmented populations. *Conservation Biology* **8**:50–59.
- Forman, R. T. T., and M. Godron. 1986. *Landscape ecology*. John Wiley & Sons, New York.
- Franklin, J. F., and R. T. T. Forman. 1987. Creating landscape patterns by forest cutting: ecological consequences and principles. *Landscape Ecology* **1**:5–18.
- Frederickson, R. J. 1990. The effects of disease, prey fluctuation, and clear-cutting on American martens in Newfoundland, Canada. M.S. thesis. Utah State University, Logan.
- Gilmer, D. G., L. M. Cowardin, R. L. Duval, L. M. Cechlin, and C. W. Shaiffer. 1981. *Procedures for the use of aircraft in biotelemetry studies*. Resource publication 140. U.S. Fish and Wildlife Service, Washington, D.C.
- Hagan, J. M., W. M. Vander Haegen, and P. S. McKinley. 1996. The early development of forest fragmentation effects on birds. *Conservation Biology* **10**:188–202.
- Hargis, C. D. 1996. The influence of forest fragmentation and landscape pattern in American martens and their prey. Ph.D. dissertation. Utah State University, Logan.
- Hargis, C. D., and J. A. Bissonette. 1997. Effects of forest fragmentation on populations of American marten in the intermountain west. Pages 437–451 in G. Proulx, H. N. Bryant, and P. M. Woodard, editors. *Martes: taxonomy, ecology, techniques and management*. Provincial Museum of Alberta, Edmonton, Canada.
- Hargis, C. D., and D. R. McCullough. 1984. Winter diet and habitat selection of marten in Yosemite National Park. *Journal of Wildlife Management* **48**:140–146.
- Harris, L. D. 1984. *The fragmented forest: island biogeography theory and the preservation of biotic diversity*. University of Chicago Press, Chicago.
- Harrison, D. J., and N. E. Famous. 1991. Effects of peat harvesting on a large mammalian carnivore: a case study with coyotes (*Canis latrans*). Pages 77–96 in D. N. Grubich and T. J. Malterer, editors. *Proceedings of the International Peat Symposium*, Natural Resources Research Institute, Duluth, Minnesota.
- Hodgman, T. P., D. J. Harrison, D. D. Katnik, K. D. Elowe. 1994. Survival in an intensively trapped marten population in Maine. *Journal of Wildlife Management* **58**:593–600.
- Hodgman, T. P., D. J. Harrison, D. M. Phillips, and K. D. Elowe. 1997. Survival of American marten in an untrapped forest preserve in

- Maine. Pages 86–99 in G. Proulx, H. N. Bryant, and P. M. Woodard, editors. *Martes: taxonomy, ecology, techniques and management*. Provincial Museum of Alberta, Edmonton, Canada.
- Hunter, M. L. 1990. *Wildlife, forests, and forestry: principles of managing forests for biological diversity*. Prentice Hall, Englewood Cliffs, New Jersey.
- Katnik, D. D. 1992. Spatial use, territoriality, and summer-autumn selection of habitat in an intensively harvested population of martens on commercial forestland in Maine. M.S. thesis. University of Maine, Orono.
- Katnik, D. D., D. J. Harrison, and T. P. Hodgman. 1994. Spatial relations in a harvested population of martens in Maine. *Journal of Wildlife Management* 58:600–607.
- McCormack, M. L., Jr. 1994. Reductions in herbicide use for forest management. *Weed Technology* 8:344–349.
- McGarigal, K., and B. Marks. 1995. FRAGSTATS: spatial pattern analysis program for quantifying landscape structure. General technical report PNW-GTR-351. U.S. Forest Service, Pacific Northwest Research Station, Portland, Oregon.
- Mills, L. S. 1995. Edge effects and isolation: red-backed voles on forest remnants. *Conservation Biology* 9:395–403.
- Mohr, C. O. 1947. Table of equivalent populations of North American small mammals. *American Midland Naturalist* 37:223–249.
- Odum, E. P., and E. J. Kuenzler. 1955. Measurement of territory and home range size in birds. *Auk* 72:128–137.
- Phillips, D. M. 1994. Social and spatial characteristics, and dispersal of marten in a forest preserve and industrial forest. M.S. thesis. University of Maine, Orono.
- Powell, R. A. 1994. Structure and spacing of *Martes* populations. Pages 101–121 in S. W. Buskirk, A. S. Harestad, M. G. Raphael, and R. A. Powell, editors. *Martens, sables, and fishers: biology and conservation*. Cornell University Press, Ithaca, New York.
- Pulliam, H. R. 1988. Sources, sinks, and population regulation. *The American Naturalist* 132:652–661.
- Sandell, M. 1989. The mating tactics and spacing patterns of solitary carnivores. Pages 164–182 in J. L. Gittleman, editor. *Carnivore behavior, ecology, and evolution*. Cornell University Press, Ithaca, New York.
- Sherburne, S. S., and J. A. Bissonette. 1994. Marten subnivean access point use: response to subnivean prey levels. *Journal of Wildlife Management* 58:400–405.
- Smith, A. T. 1974. The distribution and dispersal of pikas: consequences of insular population structure. *Ecology* 55:1112–1119.
- Snyder, J. E., and J. A. Bissonette. 1987. Marten use of clear-cuttings and residual forest stands in western Newfoundland. *Canadian Journal of Zoology* 65:169–174.
- Soutiere, E. C. 1979. Effects of timber harvesting on marten in Maine. *Journal of Wildlife Management* 43:850–860.
- Spencer, W. D., R. H. Barrett, and W. J. Zielinski. 1983. Marten habitat preferences in the northern Sierra Nevada. *Journal of Wildlife Management* 47:1181–1186.
- Stevenson, J. D., and J. T. Major. 1982. Marten use of habitat in a commercially clear-cut forest. *Journal of Wildlife Management* 46:175–182.
- Thompson, I. D. 1994. Marten populations in uncut mature and post-logging boreal forests in Ontario. *Journal of Wildlife Management* 57:272–280.
- Thompson, I. D., and P. W. Colgan. 1994. Marten activity in uncut and logged boreal forests in Ontario. *Journal of Wildlife Management* 58:280–288.
- Van Horne, B. 1983. Density as a misleading indicator of habitat quality. *Journal of Wildlife Management* 47:893–901.
- White, G. C., and R. A. Garrott. 1984. Portable computer system for field processing biotelemetry triangulation data. Information leaflet 110. Colorado Division of Wildlife and Game, Fort Collins, Colorado.
- White, G. C., and R. A. Garrott. 1990. Analysis of wildlife radio-tracking data. Academic Press, San Diego, California.
- Wilcove, D. S., C. H. McLellan, and A. D. Dobson. 1986. Habitat fragmentation in the temperate zone. Pages 237–256 in M. E. Soulé, editor. *Conservation biology: the science of scarcity and diversity*. Sinauer Associates, Sunderland, Massachusetts.
- Wynne, K. M., and J. A. Sherburne. 1984. Summer home-range use by adult marten in northwestern Maine. *Canadian Journal of Zoology* 62:941–943.
- Yahner, R. H. 1988. Changes in wildlife communities near edges. *Conservation Biology* 2:333–339.

